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Plate 1. Type Specimen of Balsamorhiza terebinthacea (Hook.) Nutt.

THE RELATIONSHIP BETWEEN QUERCUS DUMOSA AND QUERCUS TURBINELLA

John M. Tucker

Quercus turbinella Greene and *Q. dumosa* Nutt. are closely related oaks; both commonly occur as chaparral shrubs, and both have small, hard, evergreen leaves which are very similar in shape. Although similar in these respects, in their most distinctive states they exhibit a number of differences—morphological, ecological, and geographical. Their ranges overlap in southern California, however, and in this area they intergrade to a greater or lesser degree. The purpose of this paper is to record the results of a study of this intergradation. The author's opinions regarding their taxonomic treatment are presented elsewhere (Tucker, 1952).

Differences between Quercus dumosa and Q. turbinella

The range of *Q. dumosa* and that of the typical subspecies of *Q. turbinella* are evidently completely disjunct. The latter occurs in California only in the New York Mountains of eastern San Bernardino County, ranging eastward to western Texas and recurring in northern Baja California (the type locality). *Quercus dumosa* does not occur as far east as the New York Mountains, and in Baja California it is apparently isolated from *Q. turbinella*.

The Californian subspecies (*Q. turbinella* subsp. *californica* Tucker) does, however, overlap the range of *Q. dumosa*, although ecologically they are in large part separated from one another. *Quercus turbinella californica* is the scrub oak component of the pinyon pine-juniper association of arid mountain slopes near or bordering the western edge of the Mohave Desert, and also occurs in the more arid parts of the inner South Coast Ranges. *Quercus dumosa* is a common element of the slightly more mesic chaparral of semi-arid, interior mountain slopes of southern California (although its range extends northward as far as Tehama County). Where these associations meet in interior southern California, the two oaks tend to intergrade.

In gross aspect *Q. dumosa* and *Q. turbinella* subsp. *californica* are quite similar in several respects. In their most distinctive states, however, they differ in a number of morphological characteristics, as follows:

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN QUERCUS TURBINELLA CALIFORNICA AND Q. DUMOSA.

Q. turbinella californica	*Q. dumosa*
1. Upper leaf surface gray to gray-green; dull, not shining	1. Upper leaf surface green and shining
2. Leaf margin spinose-dentate (teeth with definite short spines to 1 mm. long)	2. Leaf margin usually mucronate-dentate to entire or subspinose; only infrequently definitely spinose
3. Twigs of the current season densely yellow-gray tomentose	3. Twigs of the current season pubescent to glabrate and brownish
4. Acorn cups thin	4. Acorn cups thick
5. Cup scales scarcely (or not at all) tuberculate	5. Cup scales (especially basal ones) usually strongly tuberculate
6. Cups turbinate to subhemipheric (or deeply cup-shaped) but the margins not turning inward	6. Cups hemispheric to about ⅔ spherical, the margins tapering inward

They tend to differ also in the size and shape of their buds and the shape of their acorns. In *Q. turbinella* the mature terminal buds are commonly small (1–2 mm. long) and globose, where as in *Q. dumosa* they are larger and usually ovoid. Acorns of the former are relatively slender and taper gradually to the pointed apex; those of the latter are broader in proportion to their length, and roundish at the apex.

Classification of these oaks has varied considerably with different authors. Some have regarded them as two distinct species; others have treated *Q. turbinella* as a variety of *Q. dumosa* (the older name); and still others have considered *Q. turbinella* to be merely a form of *Q. dumosa* unworthy of even varietal status (for a more detailed discussion of their taxonomic history see Tucker, op. cit.). As evidenced by their morphological similarity, it has been generally acknowledged that a close relationship exists between them. Their intergradation, however, has probably been the major factor causing some authors to treat them as elements of a single species.

Thanks are due the curators of the following herbaria for the loan of specimens: Pomona College (POM); San Diego Society of Natural History Herbarium (SD); University of

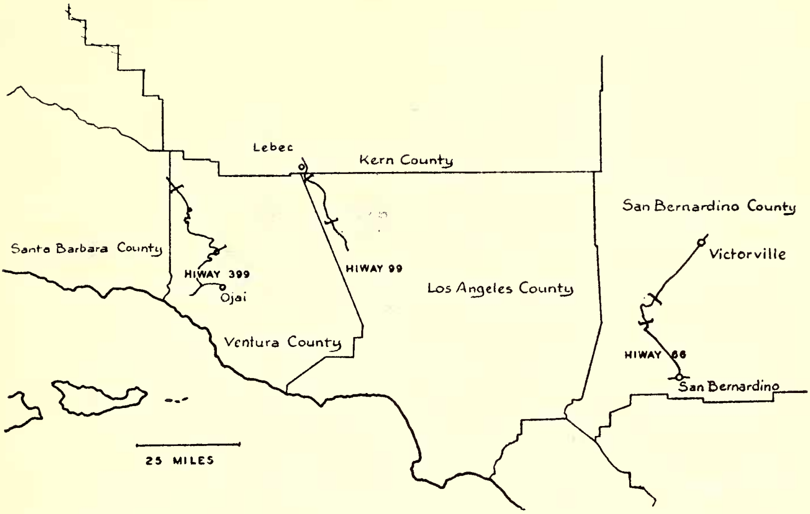

FIG. 1. Location of transects across zone of intergradation between *Quercus turbinella* and *Q. dumosa* in southern California.

California, Berkeley (UC); and University of California, Los Angeles (LA). Specimens in the writer's personal collection are cited by his initials (JMT).

Population Samples

In order to obtain more pertinent and detailed data than was possible from the study of miscellaneous herbarium specimens alone, three series of population samples ("mass collections"; cf. Anderson, 1941) were collected in southern California along transects across the zone of intergradation (fig. 1). The series along Highway 399 over Pine Mountain in northwestern Ventura County was collected on February 16, 1946, by Dr. G. L. Stebbins, Jr., Dr. C. H. Muller, and Mr. Clifton Smith. The other two were collected by the author with the help of his wife—one on October 18 and 19, 1946, along the Ridge Route (Highway 99) in northwestern Los Angeles County, the other on October 20, 1946, along Highway 66 over Cajon Pass in southwestern San Bernardino County. The location and the number of individuals in each population sample are given in Table 2.

For the analysis of these collections a hybrid index (cf. Anderson, 1936; Goodwin, 1937; Heiser, 1947; and Stebbins et al, 1947) was constructed on the basis of the six differences between *Q. turbinella californica* and *Q. dumosa* listed in Table 1. Since these differences were not all of the same degree or constancy, the characters were not all assigned the same index values. In each case the minimum value is characteristic of *Q. turbinella,* and the maximum is characteristic of *Q. dumosa.* During this analysis, "standard" specimens of *Q. dumosa, Q.*

TABLE 2. POPULATION SAMPLES OF QUERCUS DUMOSA AND Q. TURBI-CALIFORNICA.

Collection number	No. of individuals in sample	Location
Pine Mountain Transect, Ventura County (fig. 2).		
3607[1]	20	upper Cayama Valley, 6.6 mi. north of Lockwood Valley Rd.
3608	23	north base of Pine Mountain, .3 mi. south of Lockwood Valley Rd.
3609	20	north slope of Pine Mountain, 3 mi. south of Lockwood Valley Rd.
3610	17	north side of Pine Mountain, .5 mi. north of summit
3614	18	along Sespe Creek, 17.4 mi. north of Wheeler's Hot Springs
3615	21	along Sespe Creek, 15.7 mi. north of Wheeler's Hot Springs
3616	28	along Sespe Creek, 14.2 mi. north of Wheeler's Hot Springs
3617	20	summit of grade between Wheeler's Hot Springs and Sespe Creek
Ridge Route Transect, Los Angeles County (fig. 3).		
1467	27	ca. 3 mi. south of Lebec, Kern Co.
1477	18	18 mi. north of Castaic
1478	30	16.9 mi. north of Castaic
1479	29	16.3 mi. north of Castaic
1480	21	16.1 mi. north of Castaic
1481	30	15.8 mi. north of Castaic
1482	21	at top of ridge, 6.4 mi. north of Castaic
Cajon Pass Transect, San Bernardino County (fig. 4).		
1483	25	7.1 mi. northeast of junction with Highway 138
1484	25	4.8 mi. northeast of junction with Highway 138
1485	20	1.9 mi. southeast of junction with Highway 138

[1]Collection numbers in the Pine Mountain Transect are those of G. L. Stebbins, Jr.; in the Ridge Route and Cajon Pass transects they are those of the author.

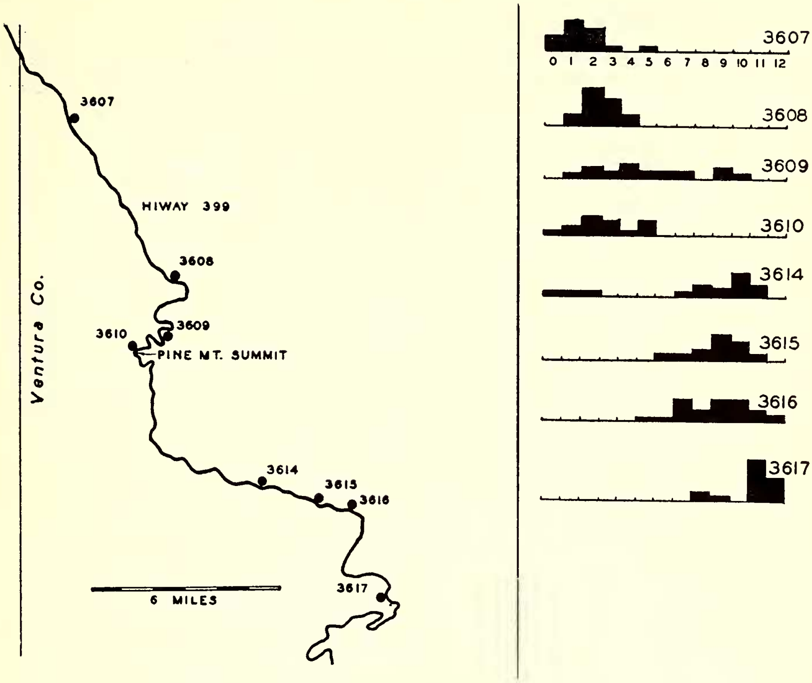

FIG. 2. Pine Mountain Transect, Ventura County.

turbinella californica, and intermediates were kept at hand for comparison. Each individual was scored on the six characters, the sum of these scores representing an index total for that particular plant. The totals for each population sample are presented in the form of a histogram.

Ratings on the six differences were as follows:

1. *Leaf color.* This is the most sharply distinct difference; hence a wider range between extremes of index scores, 0 to 4, was allowed than on any of the others.

2. *Leaf margin.* Three categories were recognized, scoring 0 to 2.

3. *Twig pubescence.* Since, in either oak, this is somewhat more variable than the other characters, only two categories were recognized, scoring 0 and 1.

4. *Thickness of acorn cup.* Three categories were recognized, scoring 0 to 2.

5. *Cup scales.* Three categories were recognized, scoring 0 to 2.

6. *Cup shape.* Since these oaks are not sharply separated on this difference, only two conditions were recognized, scoring 0 and 1.

RESULTS AND DISCUSSION

In the histograms in figs. 2, 3, and 4, index totals are shown by the horizontal scale, and the number of plants is indicated

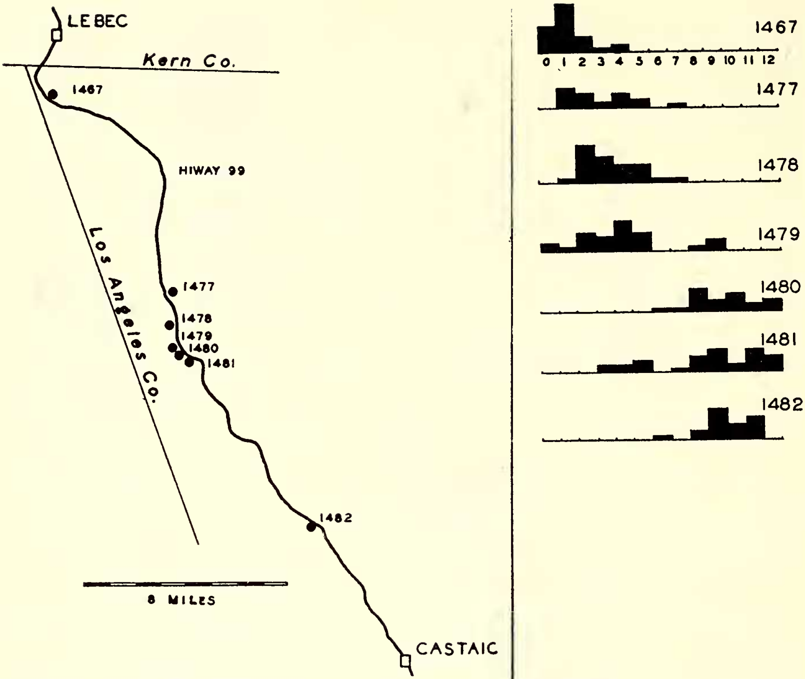

FIG. 3. Ridge Route Transect, Los Angeles County.

by the heights of the vertical columns. For the sake of discussion and comparison, individuals whose totals fall in the five lowest classes (0–4 inclusive) will be considered "good" *Q. turbinella,* since characters of this species received low scores. The "purest" collection of the latter made in this study, *Tucker 1467,* exhibits this range of index totals (fig. 3). Those whose totals fall in the five highest classes (8–12 inclusive) will be considered "good" *Q. dumosa,* since characters of this species received high scores. The "purest" collection, *Stebbins 3617,* exhibits this range (fig. 2). The remaining classes, of course, comprise the intermediate range.

In analyzing certain of these population samples, it seemed that cup characters often varied widely within the sample, while leaf characters were more consistent. To determine the degree of correlation between foliage and cup characters, therefore, a series of scatter diagrams was plotted (fig. 5). For each individual the total score on cup characters was plotted (as the ordinate) against the total on leaf and twig characters (as the abscissa).

PINE MOUNTAIN TRANSECT (figs. 2 and 5A). It is evident that *Stebbins 3607* is a collection of essentially "good" *Q. turbinella,* and, conversely, that *Stebbins 3617* is a collection of "good" *Q. dumosa.* Plotted on the same base line, they would present a discontinuous distribution, which indicates that, as they

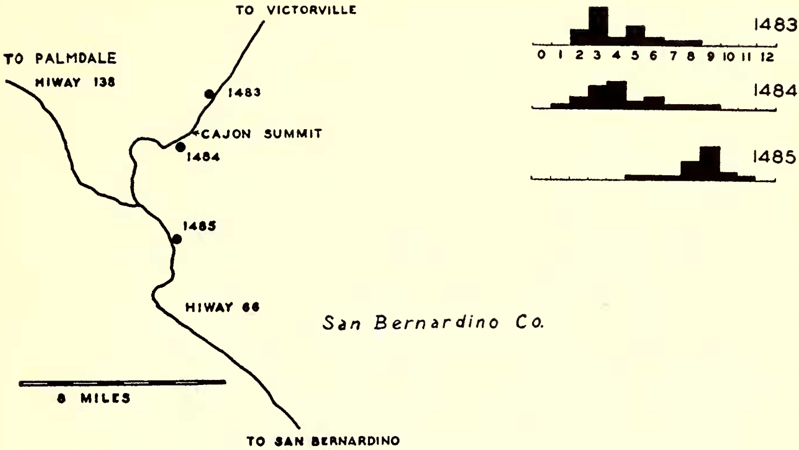

FIG. 4. Cajon Pass Transect, San Bernardino County.

occur in their respective habitats, they are morphologically quite distinct in the aggregate of characters scored.

Most of the other collections have a larger proportion in the intermediate range. Indeed, in *Stebbins 3609* the intermediates form a nearly continuous series between *Q. turbinella* and *Q. dumosa.* On the other hand, in *Stebbins 3614,* which also includes individuals of both species, there is only one *Q. dumosa*-like individual in the intermediate range.

These data indicate that in an occasional population along this transect the morphological gap between *Q. turbinella* and *Q. dumosa* may be bridged by intermediates, but this is not always the case. Any given population usually is composed mainly of one entity or the other, together with some intermediates. The presence of these intermediates suggests that populations of *Q. turbinella* and *Q. dumosa* have been reciprocally modified through introgression.

The scatter diagrams (fig. 5A) for this transect reveal one interesting point. In the collections that are predominantly *Q. dumosa* on the basis of index totals (*Stebbins 3614–3617*), the total scores on cup characters alone are distinctly more variable than the totals on leaf and twig characters. In *Stebbins 3616,* for example, all the leaf and twig totals lie in the higher (*Q. dumosa*) half of the range; the cup totals, however, are spread over the entire range. On the other hand, the collections that are predominantly *Q. turbinella* (*Stebbins 3607–3610*) do not show any conspicuous difference in variability between cup totals and leaf and twig totals. A tentative explanation is given following discussion of the other two transects.

RIDGE ROUTE TRANSECT (figs. 3 and 5B). On this transect two points of similarity to the preceding are apparent. (1) The first and last collections, *Tucker 1467* and *1482,* are fairly representative *Q. turbinella* and *Q. dumosa*, respectively. (2) All the other collections, *Tucker 1477–1481,* have a higher proportion of intermediates than do the terminal collections. This suggests that the populations from which *Tucker 1477–1481* were collected have been modified through introgression. Even so, in the two populations in which both entities occur (*Tucker 1479* and *1481*), they are separated by evident, although narrow, morphological gaps. The change from populations of *Q. turbinella* to populations of *Q. dumosa* is thus not a gradual merging of one into the other, but a fairly abrupt shift.

As in the preceding transect, the scatter diagrams reveal that in collections that are predominantly *Q. dumosa,* the cup totals are more variable than the leaf and twig totals. In *Tucker 1481,* for example, if we disregard the individuals of *Q. turbinella* and *Q. turbinella*-like intermediates, it is apparent that the others all have leaf and twig totals of 6 or 7 ("good" *Q. dumosa*), while the cup totals extend over the entire range. The collections that are predominantly *Q. turbinella,* however, do not show this difference in variability.

Cajon Pass transect (figs. 4 and 5c). In fig. 4 both terminal collections show a higher proportion of intermediates than corresponding collections on the preceding transects. Nevertheless, *Tucker 1483* represents the "purest" *Q. turbinella* along this transect, being a sample of the first oaks encountered as one ascends from the desert toward Cajon Pass. Here, *Q. turbinella* was growing in association with *Juniperus californica, Artemisia tridentata,* and *Yucca* sp. *Tucker 1485,* the only collection of *Q. dumosa,* was isolated from *Q. turbinella* by a gap of several miles along this transect (although they may overlap elsewhere in this general area). At the location of *Tucker 1485, Q. dumosa* was growing in association with *Adenostoma fasciculatum, Ceanothus crassifolius,* and *Quercus Wislizenii.*

It is obvious that the intermediate part of the range is completely bridged in all three histograms. The greater intermediacy of these collections as compared with those of the preceding transects strongly suggests that introgression has effected a greater merging of *Q. turbinella* and *Q. dumosa* in this area.

As in the preceding transects, the scatter diagram for the single collection of *Q. dumosa* on this transect (*Tucker 1485*) shows the leaf and twig totals to be much less variable than the cup totals. Once again, this is not the case in the collections that are predominantly *Q. turbinella* (*Tucker 1483* and

Explanation of Fig. 5.

Fig. 5. Scatter diagrams of the three transect area populations showing total scores on cup characters (plotted as ordinates) and total scores on leaf and twig characters as the abscissae). Individuals with a preponderance of *Q. turbinella* characters fall to the lower left and those with a preponderance of *Q. dumosa* to the upper right.

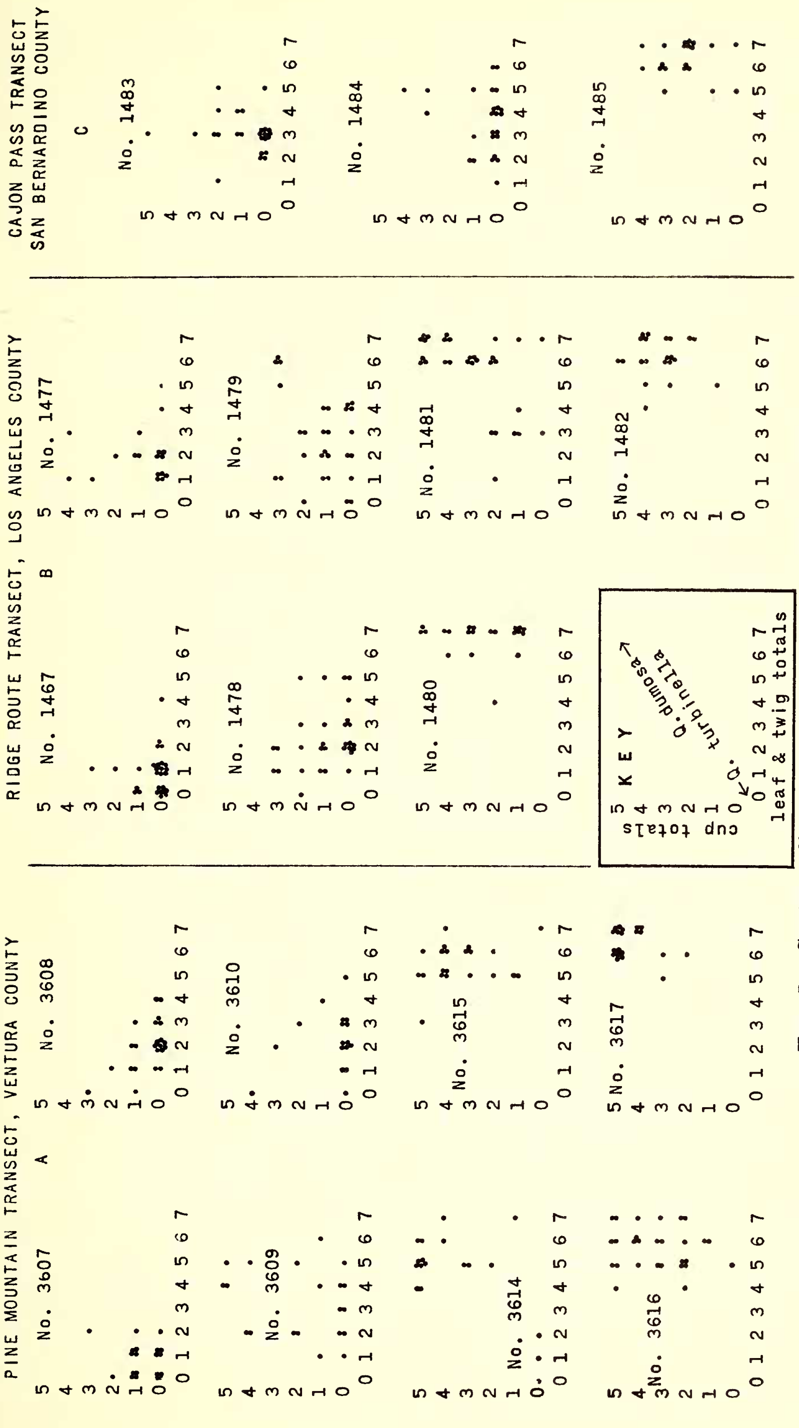

FIG. 5. Scatter diagrams of the three transect area populations.

1484). In the latter, cup totals are not conspicuously more variable than leaf and twig totals.

As a tentative explanation of the preceding observations it may be suggested that in the habitats in which *Q. dumosa* predominates, its glossy, green leaves (and perhaps the other leaf and twig characters, also—or genetically linked physiological characteristics) may have a higher selective value than the corresponding characters of *Q. turbinella*. Glossy, green foliage is rather frequent in species of the chaparral formation in which *Q. dumosa* occurs, *Prunus ilicifolia, Rhamnus crocea*, and *Ceanothus sorediatus* being common examples. Foliage of this aspect is rather infrequent in desert-border habitats, whereas pale grayish foliage (which, indeed, characterizes *Q. turbinella*) is much more common. It should be borne in mind that selection would exert its earliest effects during the critical establishment stage—the first year or two in the life of a young seedling. Selection at this time would act upon foliage characters, not fruit characters. The latter, obviously, would not be manifested until some years later. If genetic linkage between factors for the cup characters studied and those for the foliage characters studied were only slight (as seems to be the case), then a wide variety of cup characters could become established in a heterozygous population, which, due to rather stringent selection, was much more uniform for foliage characters.

On the other hand, in the more arid habitats where the ranges of these two oaks overlap, one would expect that foliage characters of *Q. turbinella* would have a selective advantage. Be that as it may, the scatter diagrams for such collections as *Tucker 1478* and *1479* (fig. 5B), indicate that *Q. dumosa* genes for both foliage and cup characters have become established in these populations. *Quercus turbinella* genes, conversely, have modified populations of *Q. dumosa* for the most part only in cup characters. In areas where reciprocal introgression has occurred, therefore, the flow of *Q. dumosa* genes into the *Q. turbinella population* has been more pronounced than the reverse.

Although the author has not had the opportunity to study *Q. turbinella* in the field farther south than Cajon Pass, a number of herbarium specimens have been seen from elsewhere in San Bernardino County, and from Riverside and San Diego counties. Just as on the desert slopes north of Cajon Pass, collections from the north slope of the San Bernardino Mountains, though more like *Q. turbinella*, usually show some suggestion of *Q. dumosa*. Eastward and southeastward from the San Bernardino Mountains, characters of *Q. dumosa* are even more prevalent. Although one specimen of fairly characteristic *Q. turninella* has been seen from Morongo Pass (*Epling* and *Robison*, June 24, 1933, LA), most collections from this area and from the Little San Bernardino Mountains to the southeast exhibit mixtures of the characters of both, and some are nearer to *Q. dumosa.*

The few specimens seen from the Cottonwood and Eagle mountains of Riverside County, although they also contain mixtures of characters of the two, are in general nearer to *Q. dumosa.* These are: Cottonwood Mts., Colorado Desert, *Jaeger,* June, 1921 (UC); north slope of Eagle Mountains, Riverside County, *Alexander* and *Kellogg 2210* (UC); Monsen Canyon, Eagle Mountains, *Alexander* and *Kellogg 2243,* (UC); Palm Canyon, Eagle Mts., *Jaeger,* Dec. 20, 1927 (POM). The single specimen seen from the Santa Rosa Mountains (road from Deep Canyon to Vandeventer Flat, *Munz 12845* (POM), and most of the material from desert-border mountains of San Diego County exhibit a preponderance of *Q. dumosa* characters. An occasional specimen may have paler leaves than usual, e.g. Boulder Park, four miles east of Jacumba, *Dixon 341* (JMT), or thin, only slightly tuberculate cups: Boulder Park, Imperial County, *Gander 4662* (SD). Nevertheless, even those specimens most similar to *Q. turbinella* are distinctly intermediate in the aggregate of their characters. Judging by specimens of *Q. dumosa* from central and western San Diego County, it seems probable that there is complete intergradation with the desert-border forms. In the author's opinion, the material from desert-border mountains of Riverside and San Diego counties is best referred to *Q. dumosa* rather than to *Q. turbinella* (as such specimens have frequently been determined). This pattern of morphological variation suggests that *Q. dumosa* is "swamping out" *Q. turbinella* in these areas. More intensive study is required, however, before this matter can be settled.

Conclusions

1. In the areas of the three transects sampled, *Q. dumosa* and *Q. turbinella* have both become modified through interbreeding (introgression).
2. Along the Pine Mountain and Ridge Route transects, despite the introgression, the species still tend to retain their respective morphological identities.
3. In general, greater modification has taken place in both *Q. dumosa* and *Q. turbinella* along the Cajon Pass transect than along the other transects.
4. Eastward and southeastward from the area of Cajon Pass, *Q. dumosa* characters tend more and more to predominate (judging by miscellaneous herbarium specimens). Indeed, most collections from desert-border mountains of Riverside and San Diego counties are, in general, more similar to *Q. dumosa* than to *Q. turbinella.*

University of California, Davis.
Department of Botany,

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A CORRECTION IN THE STATUS OF VIOLA MACLOSKEYI

Milo S. Baker

In the January, 1953, issue of Madroño I proposed uniting the two white violets known as *Viola pallens* (Banks ex DC.) Brainerd and *V. Macloskeyi* Lloyd and made two combinations under *V. pallens,* which, because of the rule of priority, are not valid. To comply with this rule, it is necessary, much to my regret, to abandon the name *pallens,* so much older in the varietal category, in favor of the earlier specific name *V. Macloskeyi* Lloyd, since the latter has ten years priority over *V. pallens* (Banks ex DC.) Brainerd. Hence, for all material of this species from California and Oregon, known at this time, I propose the name of *V. Macloskeyi* subsp. *Macloskeyi,* and for the northern and eastern material, the name *V. Macloskeyi* subsp. *pallens.* Formal citation for this transferal follows:

Viola Macloskeyi Lloyd subsp. **Macloskeyi.** *V. Macloskeyi* Lloyd, Erythea 3: 74. 1895. *V. blanda* var. *Macloskeyi* Jepson, Man. Fl. Pl. Calif. 648. 1925. *V. pallens* (Banks ex DC.) Brainerd subsp. *Macloskeyi* Baker, Madroño 12: 18. 1953.

Viola Macloskeyi Lloyd subsp. **pallens** (Banks ex DC.) comb. nov. *V. rotundifolia* var. *pallens* Banks ex DC. Prodr. 1: 295. 1824. *V. pallens* Brainerd, Rhodora 7: 247. 1905. *V. pallens* (Banks ex DC.) Brainerd subsp. *pallens,* Madroño 12: 17. 1953.

Santa Rosa Junior College,
Santa Rosa, California